

NEW NATURAL HYBRID COMBINATIONS AND COMMENTS ON
INTERPRETATION OF HYBRID POPULATIONS IN *CASTILLEJA*
(SCROPHULARIACEAE)

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ABSTRACT

This paper presents documentation concerning nine hybrid combinations within *Castilleja*, seven of which are new records. Published chromosome numbers for the parent taxa are summarized, and previously unpublished counts are presented for *C. flava* var. *flava*, *C. pallescens* var. *inverta*, *C. purpurea* var. *purpurea*, *C. purpurea* var. *purpurea* \times *C. indivisa*, and *C. viscidula*. The hybrid records are interpreted in the light of chromosome analysis. Speculation is made concerning the significance of these records and of hybrid populations in general in understanding the evolution and taxonomy of this genus.

KEY WORDS: *Castilleja*, Scrophulariaceae, hybridization, chromosome numbers

Interspecific hybridization in the genus *Castilleja* is well known, both in natural populations (*e.g.*, Heckard 1968; Heckard & Chuang 1977) and in greenhouse studies (Heckard 1964). Hybridization is widely recognized for its role in speciation, taxonomic complexity, and the difficulty of specimen identification within this genus (Heckard 1964, 1968; Holmgren 1971, 1984; Ownbey 1959).

In the course of my field studies of the impressive diversity within *Castilleja*, I have made a number of collections of plants that appear to be hybrid combinations between various recognized taxa occurring in the given area. These plants are apparently all either single-specimen first generation hybrids or localized hybrid swarms. To my knowledge, none of these hybrid forms has been recorded previously in the literature, except for the last two hybrids listed

below. Their recognition here serves to further underscore both the ease and importance of hybridization in the evolution of this proliferating genus.

The following citations are for voucher specimens, all of which are deposited at WTU. I also cite vouchers for the putative parental species when these were found within the same local population. A few of the records listed below lack voucher specimens, but all plants mentioned are documented with detailed color photographs, which are on file in my personal collection.

1. *Castilleja peckiana* Pennell \times *Castilleja oresbia* Greenm. Oregon: Grant Co.: along U.S. Hwy. 395, ca. 0.4 km N of Beech Creek Summit, in brushy field at interface of open area dominated by *Artemesia tridentata* with broken forest of *Pinus ponderosa*, T11S, R30E, sect. 32, 1,426 m, 2 June 1986, *M. Egger 191*.

At this site were at least two obvious F_1 hybrids, and the voucher sheet contains a stem from each plant. Both hybrid individuals grew within 1 m of apparently pure individuals of both *Castilleja peckiana* (*M. Egger 192*) and *Castilleja oresbia* (*M. Egger 190*). The hybrids are intermediate between the putative parents in many respects, including bract color (dull pale orange), length of beak, overall corolla length, calyx incision, and general aspect.

Castilleja peckiana is known to be a polyploid species, with published chromosome counts of $n=36$, $n=48$, and $n=60$ (Heckard 1968). It is thought that *C. peckiana* is, itself, of hybrid origin, possibly incorporating the genomes of several species (Heckard 1968; Holmgren 1984). As far as I know, no published chromosome counts exist for *Castilleja oresbia*, but it is thought to be involved in the hybrid origin of *Castilleja zanthotricha* Pennell (Holmgren 1971), which is known to have a count of $n=24$ (Heckard & Chuang 1977). The closest relatives of *C. oresbia* are *Castilleja thompsonii* Pennell and *Castilleja pallescens* (A. Gray) Greenm. The former is known to have counts of $n=12$ and $n=24$, and the latter is known from a count of $n=24$ (Heckard & Chuang 1977), as well as from a previously unpublished count by F.M. and T.I. Chuang of $n=12$ taken from my collection, Idaho: Custer Co.: Lost River/Pahsimeroi Mountains, flats of high sagebrush valley ca. 2.4 km SW of Doublesprings Pass, T10N, R22E, Sect. 16, ca. 2120 m, 22 June 1990, *M. Egger 321* (L.R. Heckard, pers. comm. 1990).

2. *Castilleja lanata* A. Gray \times *Castilleja sessiliflora* Pursh. Texas: Pecos Co.: in grassy median-strip meadow along exit from eastbound I-10 onto U.S. Hwy. 190 to Iraan, ca. 800 m, 5 April 1990, *M. Egger 302 & 304*.

These two specimens represent stems from two different plants from a fairly uniform local population of 30-40 individuals, which appear to represent a self-perpetuating localized hybrid swarm. Neither putative parent species is represented in pure form in this population, though an extensive and vigorous population of very typical *Castilleja lanata* is found along U.S. Hwy. 190 about

0.4 km N of the hybrid population (M. Egger 303). *Castilleja sessiliflora* is also common in Pecos Co. (Nesom 1992).

The putative hybrid plants have the stature and growth form, deep secondary calyx clefts, and petaloid, shelf-like lower corolla lip of *Castilleja sessiliflora*, combined with the heavily lanate stem pubescence and the corolla tube and beak proportions of *C. lanata*. The plants are intermediate in bract shape and inflorescence coloration, the latter being an odd shade of pale rose, apparently combining the bright red of *C. lanata* with the pale pink-violet of the "purpurina" form of *C. sessiliflora* common in this portion of Texas.

The only published chromosome counts are of $n=12$ for *Castilleja lanata* (Ward 1983; Chuang 1993), as well as for *C. sessiliflora* (Heckard & Chuang 1977; Löve & Löve 1982; Freeman & Brooks 1988). Despite the fact that the common diploid state of these species could facilitate relatively easy hybridization, the existence of a hybrid swarm population derived from these two only distantly related species within the genus is testimony to the evolutionary plasticity and significance of hybridization in *Castilleja*. It may well be that hybrid swarms such as this led eventually to the genetic and phenotypic consolidation of such hybrid taxa as *C. dissitiflora* N. Holmgren, *C. montigena* Heckard and *C. xanthotricha*, especially when a polyploid swarm "emerges" from the hybridization of two diploid species. A thorough census of *Castilleja* in this portion of Pecos Co. for the possible existence of additional populations of this hybrid would be informative, as would a chromosome count for the documented population to determine its ploidy level.

3. *Castilleja scabrida* Eastw. var. *scabrida* \times *Castilleja linariifolia* Benth. Utah: Garfield Co.: Dixie National Forest, ca. 0.8 km. E of Hell's Backbone Bridge, loose sandstone roadside bank along F.S. Rd. 153, T33S, R3E, sect. 5, ca. 2740 m, 28 June 1985, M. Egger 114.

This collection is from a single large multi-stemmed F_1 hybrid. Adjacent to this individual grew several apparently pure plants of both *Castilleja scabrida* (M. Egger 119) and *C. linariifolia* (M. Egger s.n.). The hybrid plant combined the stature, growth form, corolla dimensions, and pubescence of stem, herbage and inflorescence typical of *C. scabrida* with the thin, elongate leaves and strongly unequal primary calyx clefts of *C. linariifolia*.

Known chromosome counts for *Castilleja scabrida* are $n=12$ (Heckard & Chuang 1977), and for *C. linariifolia*, counts are of $n=12$ and $n=24$ (Heckard 1958, 1968; Heckard & Chuang 1977).

4. *Castilleja viscidula* A. Gray \times *Castilleja flava* S. Watson var. *flava*. Nevada: Elko Co.: Independence Range, ridge top about 300 m NW of crest of road at Jack Creek Summit, T42N, R53E, Sect. 10, NW 1/4, 2,377 m, 24 June 1990, M. Egger 334.

A single apparent F_1 hybrid plant was found growing within a fairly dense

but highly localized population of *Castilleja viscidula* (M. Egger 333), surrounded by and occasionally intermixed with more scattered plants of *C. flava* var. *flava* (M. Egger 329). The hybrid plant combines several key features of both species, such as the lemon-yellow bracts of *C. flava* var. *flava* and the crisped leaf margins of *C. viscidula*. Corolla measurements are intermediate.

Previously unpublished chromosome counts of $n=12$ for the above-cited specimen of *Castilleja viscidula* and $n=24$ for *Castilleja flava* var. *flava* were obtained by F.M. and T.I. Chuang, but buds collected from the hybrid plant were too old for chromosome determination (L.R. Heckard, pers. comm. 1990). Published counts for *C. viscidula* are all of $n=12$ (Holmgren 1971; Reveal & Styer 1973), except for one count of $n=36$ (Heckard & Chuang 1977) from an area of hybridization with "*Castilleja lapidicola* Heller" (= *Castilleja nana* Eastw.). *Castilleja flava* var. *flava* is known only from counts of $n=24$ (Heckard 1968; Heckard & Chuang 1977). Thus, it is likely that the hybrid plant violates the generalization that different ploidy levels prevent hybridization. On the other hand, the population as a whole exhibits no noticeable introgression between the two parent taxa, so the hybrid barrier must be effective generally at maintaining species identities in this case.

5. *Castilleja lutescens* (Greenm.) Rydb. \times *Castilleja hispida* Benth. var. *acuta* (Pennell) Ownbey. Oregon: Garfield Co.: Umatilla National Forest, SW of Peola, E edge of Pataha Bunchgrass Research Natural Area, T10N, R42E, sect. 1, 1,556 m, 28 June 1988, M. Egger 229.

The hybrid plants are scattered and rare within the local population and appear to be simply occasional F_1 hybrids. The characteristics of the hybrid plants are generally intermediate. The most obvious hybrid trait is coloration of the inflorescence, which is usually very pale orange to light pink.

Pure *Castilleja lutescens* (M. Egger 228) and pure *C. hispida* var. *acuta* (M. Egger 226) are also present in this mixed population, although *C. lutescens* is by far the most numerous species. While *C. cusickii* Greenm. is also present within 100 m of the hybrid population, it does not seem to interact reproductively with the other species.

Castilleja lutescens is known to have chromosome counts of $n=24$, $n=48$, and $n=\text{ca. } 60$, while those published for *C. hispida* var. *acuta* are all of $n=48$ (Heckard 1968; Heckard & Chuang 1977).

6. *Castilleja parviflora* Bong. var. *oreopola* (Greenm.) Ownbey \times *Castilleja rupicola* Piper. Washington: Lewis Co.: Goat Rocks Wilderness Area, along Pacific Crest Trail between Elk Pass and Old Snowy Mtn., T12N, R11E, Sect. 16, SW 1/4, ca. 2,060 m, 5 August 1984, M. Egger s.n., documented photographically.

A small hybrid swarm of perhaps half a dozen plants with fairly constant characteristics was found within an area of about 25 sq. m. While not growing

in the immediate vicinity, populations of both putative parent species grow within 0.25 km of the hybrid population. The hybrid plants appear to be intermediate in most characteristics, from a reddish-magenta to salmon coloration of the bracts to the measurements and proportions of the flowering parts.

Castilleja parviflora var. *oreopola* is known from chromosome counts of $n=12$ (Heckard 1968) and $n=24$ (Baker & Parfitt 1982), while I can find no published records for *Castilleja rupicola*.

7. *Castilleja peirsonii* Eastw. \times *Castilleja lemmonii* A. Gray. California: Inyo Co.: John Muir Wilderness Area, upper Rock Creek Basin, on edge of tarn near trail between Chickenfoot Lake and Morgan Pass, T6S, R29E, Sect. 25, SW 1/4, ca. 3,330 m, 9 August 1993, M. Egger s.n., documented photographically.

A single obvious F_1 hybrid plant was found growing in a large mixed population of about 90% *Castilleja peirsonii* and 10% *C. lemmonii*. Other than for the single hybrid, the two species appear to show no intergradation at this site. The hybrid plant was intermediate in stature and foliage characteristics, and it combined the deep rose-magenta bract coloration of *C. lemmonii* with the larger, well-exserted, yellowish corolla and characteristic broad swelling of the corolla tube at the attachment of the lower lip found in *C. peirsonii*.

Published counts of chromosome numbers are of $n=12$ both for *Castilleja lemmonii* (Gillett 1954; Heckard 1968) and for *C. peirsonii* (Reveal & Spellenberg 1976). Considering that these two species share a common chromosome number, in combination with the facts that they are broadly sympatric and are frequently in flower in the same meadows at the same time, the apparent rarity of hybrids is fairly remarkable. A study of the pollination ecology of these two castillejas would be informative. *Castilleja lemmonii* is placed by Chuang & Heckard (1991) in section *Pallescentes* of subgenus *Colacus*, including species usually pollinated by bees, while *C. peirsonii* is a member of subgenus *Castilleja*, which are predominately hummingbird pollinated.

8. *Castilleja applegatei* Fernald var. *pinetorum* (Fernald) N. Holmgren \times *Castilleja chromosa* A. Nelson. California: Inyo Co.: brushy slope along road from Lone Pine to Horseshoe Meadow near pullout about 100 m W of crest of road where it levels out following switchback upgrade from Owens Valley, T17S, R36E, Sect. 7, NE 1/4, ca. 2,789 m, 26 June 1985, M. Egger 96.

This collection is of a single plant growing alone, with no other *Castilleja* in the immediate vicinity. However, both putative parent species are fairly common in this region in similar habitat. This location is near the southeastern terminus of the range of *C. applegatei* var. *pinetorum*. This hybrid combination is recorded also by Holmgren (1971).

The specimen exhibits several intermediate characteristics, while it com-

bines the divided leaves of *Castilleja chromosa* with the relatively longer corolla beak of *C. applegatei* var. *pinetorum*.

Chromosome levels recorded for the parent species include counts of $n=12$ and $n=24$ for both *Castilleja applegatei* var. *pinetorum* (Heckard 1968; Holmgren 1971) and *C. chromosa* (Heckard 1968; Heckard & Chuang 1977), so hybridization between these two species is not unexpected in the few locations where their habitat and phenology overlap.

9. *Castilleja indivisa* Engelm. \times *Castilleja purpurea* (Nutt.) G. Don var. *purpurea*. Texas: Hill Co.: W side of Hwy. I-35W, about 1.6 km S of northern boundary of Hill Co. and 5.4 km N of Itasca exit in meadowy highway right-of-way, ca. 300 m, 7 April 1990, M. Egger s.n., but unnumbered bud collections were made for chromosome analysis; hybrid plants and adjacent population are documented photographically.

At least two F_1 hybrid plants were found growing amidst a large mixed population of the two parent species consisting of about 80% *Castilleja purpurea*. The hybrid plants resemble *C. purpurea* more closely than they do *Castilleja indivisa*, but intermediate features include a red-purple cast to the bract coloration and a less divided and more rounded lobing of the leaves and bracts characteristic of the usually entire leafed *C. indivisa*.

A chromosome analysis of these two plants was conducted by F.M. and T.I. Chuang (L.R. Heckard, pers. comm. 1990). According to T.I. Chuang's notes, counts from these plants were of $n=14$ and $n=16$, which are highly unusual numbers for this genus. These unusual counts probably reflect chromosomal abnormalities resulting from the hybrid condition. The unique genetics of these plants may be a result of the cross of an annual *Castilleja* (*C. indivisa*) with a perennial from a different section of the genus. However, Nesom (1992) reports that hybrids of these two species are common in some locations in north-central Texas, with some populations showing strong introgression and character convergence. Such broad convergence was not apparent in the population from which the present specimens came. Further study is needed to understand the chromosomal interactions and characteristics of hybrid and non-hybrid populations of these two species.

Previous collections of *Castilleja indivisa* have yielded only chromosome counts of $n=12$ (Heckard 1968; Leonard *et al.* 1978), while I could find no published account of a chromosome number for *C. purpurea* var. *purpurea*. A previously unpublished count of $n=12$ for *C. purpurea* var. *citrina* was made from my collection (Texas: Kimball Co.: roadside strip along U.S. Hwy. 290, about 6.4 km W of Harper, ca. 515 m, 3 April 1990, M. Egger 294) by F.M. and T.I. Chuang (L.R. Heckard, pers. comm. 1990).

Comments on the hybrid *Castilleja* populations from the vicinity of Slate Peak, Okanogan Co., Washington

The occasionally introgressive *Castilleja* populations in this alpine area of the NE Cascades Range of Washington state (T37N, R17E, Sect. 1; T38N, R17E, Sect. 35 & 36, elev. ca. 2060 m) are of some notoriety and are the subject of several studies (Anderson & Taylor 1983; Leshner 1983; Taylor 1984). While these papers present various proposals as to the identity of the species represented in this area, the variation patterns found can be explained most efficiently by viewing these populations simply as localized assemblages of parental species (mainly *C. parviflora* Bong. var. *albida* [Pennell] Ownbey and *C. elmeri* Fernald) with occasional small patches of hybrid plants, which skew populational statistical analyses in the direction of blurring morphological species boundaries. However, based on my own admittedly non-quantitative observations of the Slate Peak populations, if one subtracts out of the statistical sample those individual plants or small groups of plants that are recognizably of hybrid nature, the problems of species character overlap appear to be minimal. With the exception of the recognizably hybrid plants, both parental species maintain their phenetic integrity reasonably well, both here and elsewhere. Thus, it seems unnecessary to evoke either a total breakdown of species boundaries or to make a tortured attempt to identify every plant strictly according to the characteristics of a published key, as proposed in Taylor (1984) and Anderson & Taylor (1993), respectively, in order to accurately represent the species composition of this area.

In the chaotic world of plant genetic systems, especially in a genus like *Castilleja* that is well known for the ease with which even species of different subgenera may hybridize, the simple fact that two species hybridize in very localized pockets where they share the same habitat need not imply that the validity of the parental species should be called into question, regardless of the outcome of statistical tests based on localized populations that may or may not reflect the nature of the species as a whole. The above conclusions regarding the nature of the Slate Peak populations are substantially in accord with the tentative conclusions of Leshner (1983) and L.R. Heckard (pers. comm. 1985).

On the other hand, it should be noted clearly that hybridization in *Castilleja* can also be more widespread, causing a nearly complete introgression of characteristics in at least portions of the zone of sympatry. The distinctions between such taxa as *C. miniata* Dougl. ex Hook. and *C. rhexifolia* Rydb. and between *C. septentrionalis* Lindley (including the synonymous *C. sulphurea* Rydb.) and *C. rhexifolia* disappear altogether in some regions of hybridization, while in other locations, the species may appear to be fairly coherent and phenetically stable (Holmgren 1984). In the case of such species pairs or groups of species, the definition of species limits must clearly depend on one's taxonomic

philosophy combined with nomenclatural conventions.

This paper is dedicated to the memory of Dr. T.I. Chuang, whose meticulous cytological and taxonomic work over several decades has greatly increased our knowledge of the systematics of the Castillejinae.

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